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THE MONTHLY CYCLING OF NUTRIENTS IN A STAND OF PINUS PINEA L.

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ABSTRACT

Nutrient uptake during growing processes in a forest ecosystem include accumulation and redistribution.

Nutrient cycling has mostly been studied on a yearly basis. In the present work, the distribution of nutrients was monitored during a sucession of shorter periods, and the final estimate of nutrient compartments and fluxes in the soil-plant system was carried out monthly and yearly.

The uptake and redistribution of five nutrients (N, K, Ca, P and Mg) were studied in a stand of Pinus pinea L., by analyzing growth phenology and productivity. Based on monthly determinations of needle biomass, and the increments of shoots, branches and boles, it was possible to determine the uptake and recycling of nutrients by the needle canopy. The fixation of the same elements in the perennial part of the phytomass was also determined monthly during the growing season, as well as their contents in the litterfall.

Using all these data, the total monthly uptake of nutrients by the trees, their immobilization in the trees, and their return to the soil as litter was quantified.

The redistribution of the same five elements by the trees on a yearly basis is also discussed. The following fluxes and compartments of the site's nutrient budget were determined: nutrient in biomass, total nutrient uptake, uptake by needles, recycling from the needles, fixation in the perennial biomass, use by reproductive components, return with litterfall.

INTRODUCTION

Almost all of the numerous studies concerning the quantification of the organic-matter cycle and the biogeochemical cycles have been based on yearly periods, with the exception of litterfall, whose seasonal rhythm required a more detailed analysis (Cole and Rapp, 1980). However, the distribution and transfer of substances and mineral elements in vegetation and in the ecosystem fluctuate continuously under the influence of various factors. Certain of these factors are biological, such as the phenology of the different species in the system, both in their growth phases and in senescence, and the activities of the fauna and the microflora. Other factors are climatic and act either directly, such as periodicity and intensity of precipitation, or indirectly, such as the influence of precipitation and temperature on biological processes.

In the present work, we concentrate more specifically on the monthly uptake of nutrients by a forest stand during one year, in order to determine its total nutrient uptake during the vegetative period. The latter is generally defined (Duvigneaud, Denaeyer De Smet, 1964) as the sum of the elements included in the woody biomass increment and in the litterfall. The first term of this sum is determined directly from the tree rings, or indirectly by dividing the perennial mineral-mass by the age of the stand. The second term is always determined directly, at least with respect to litterfall.

Beyond this annual evaluation, it is tempting to refine the description of the translocations between the various compartments of an ecosystems, or between the various components of a subsystem, by evaluating them over shorter periods, such as a month. This approach, leads not only to a comprehensive evaluation but also a succession of smaller translocations which indicate the activity of the stand or ecosystems as a function of the activity of its different components or the physical factors arising from the atmospheric and edaphic environment.

For this purpose, we have studied in a stand of *Pinus pinea* L., the phenology and monthly growth rhythm of the different components (Cabanettes, 1979 ; Cabanettes and Rapp, 1981 a), and senescence and litterfall (Rapp, 1983), both in terms of organic matter and in terms of a certain number of essential nutrients.

On the basis of *in situ* weight measurements, it is possible to refine the description and quantification of the various transfers and pathways of the nutrients between the components of the tree and throughout the whole plant-soil system.

MATERIALS AND METHODS

1. The site

The research site consisted of *Pinus pinea* L. planted on former dunes on the Mediterranean coast. The present stand was the result of a clear felling carried out in 1943. The ages of the individual trees ranged from 15 to 35 years, grouped in several populations of different ages.

The average density was 800 trees to the hectare, corresponding to 33.9 m^2 ha^{-1} of D.B.H. The average height was 10.4 m and the average circumference at 1.30 m was 63.4 cm.

2. Growth Phenology

The methods for studying variations in the phenological and dendrometric characteristics of this pine have been described in detail by Cabanettes (1979). They concern the elongation of the axes (trunk and branches), trunk-thickening and the elongation of the year's needles. All these parameters were observed for 13 consecutive months, with measurement-intervals on the order of a week.

3. Weight variations in the needles and shoots

At the same time as the elongation of needles and shoots was observed in the field, a certain number of shoots (110) were labelled at the beginning of their growth, then regularly cut until all the needles had fallen at the end of 26 months. The harvest rhythm was monthly during growing periods, and more irregular during the winter.

Each shoot was stripped of its needles, and the number and weight of the needles were determined, as well as the length and weight of the shoot.

During the period of study, the needle-shoot relationships were the following :

	one year	two years
-- average length of a shoot (cm)	44.5 ± 3.8	42.1 ± 2.1
-- number of needles per shoot	193 ± 21	181 ± 26
-- number of needles per cm of shoot	4.4 ± 0.3	4.4 ± 0.4

4. Chemical Analysis

Each shoot and an average sample of needles from each shoot were analyzed after nitroperchloric mineralization. Potassium was determined by flame photometry, and Ca and Mg by atomic absorption spectrophotometry. Phosphorus was colorimetrically assayed in the presence of ammonium nitrovanadomolybdate, and nitrogen by Kjeldahl's method.

All the results are summarized in Table 1. Each monthly result represents the mean of 4 to 10 analyses, depending on the month of sampling.

Table 1 - Variations in the chemical composition of the needles and shoots as a function of their age (% of dry matter)

	Year	Month	N	K	Ca	P	Mg
Needles	1	June	1.39	1.76	0.22	0.19	0.17
		July	1.18	1.66	0.23	0.19	0.16
		August	1.03	1.50	0.16	0.14	0.18
		September	0.87	1.13	0.16	0.12	0.16
		October	1.07	1.08	0.16	0.13	0.19
	2	February	1.19	0.96	0.19	0.14	0.19
		April	1.19	0.95	0.22	0.14	0.19
		May	1.00	0.84	0.38	0.15	0.21
		June	0.95	0.95	0.39	0.23	0.23
		July	0.95	1.01	0.45	0.20	0.23
	3	May	0.83	0.51	0.59	0.13	0.29
		July	0.75	0.72	0.59	0.13	0.27
Shoots	1	April	1.11	1.19	0.19	0.19	0.17
		May	1.05	1.17	0.25	0.17	0.20
		June	1.06	1.28	0.27	0.14	0.17
		July	0.81	0.92	0.42	0.12	0.21
		August	0.84	0.65	0.44	0.11	0.24
		September	0.57	0.65	0.51	0.08	0.20
		October	0.65	0.65	0.45	0.10	0.23
	2	February	0.52	0.49	0.44	0.08	0.20

RESULTS AND DISCUSSION

1. Phenology and growth during one year

Figure 1 shows an example of the growth rates of needles and terminal shoots during the first year, and that of trunk-thickening for the same period.

Cabanettes and Rapp (1981 a) showed that the growth phenomenon starts with the shoots, which begin lengthening in February, achieving their maximum rate (up to 9.5 mm per day) from the end of April to mid-June. The elongation stops completely at the end of this latter month. Needles appear in May, when the shoots have already reached 60 % of their final length. Elongation continues for 20 weeks, but begins to slow in the month of August. Trunk-thickening begins in March, achieving its maximum rate in April and the beginning of May (0.15 mm per day). Growth then slows, and one even observes a shrinkage in the summer, followed in September by a slight renewal of growth comparable to the increment observed in June (0.05 mm per day).

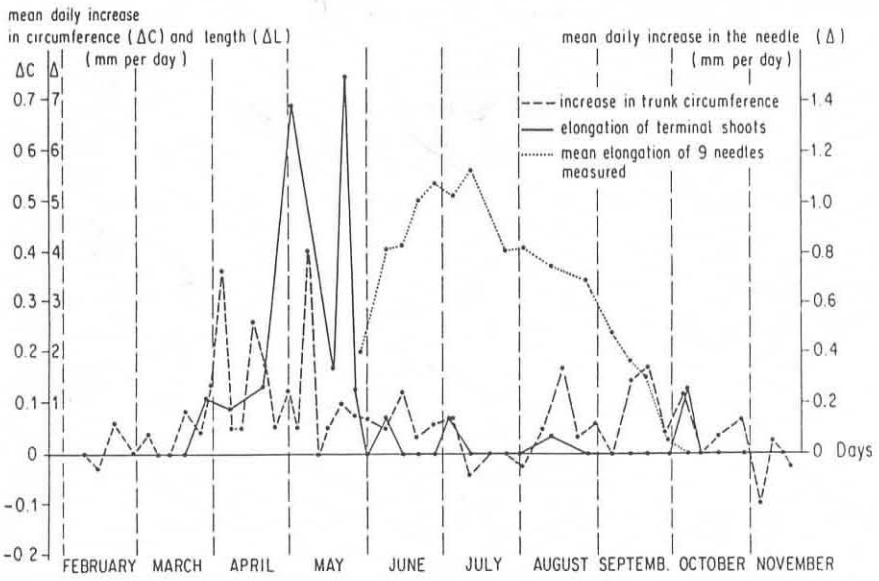

Figure 1. Comparison of growth-rate variations in the three types of growth studied.

2. Variation of the weight and mineral composition of the needles during their life-cycle

The needle-life of this pine is not restricted to the growing season, but continues in most cases for a period of two years. Most of the needles that appear in June of one year, fall to the ground two years later during June, July and August.

We studied, successively, the weight increases of a needle as a function of its age, then that of all the foliage in the stand, ending with a study of mineral-mass, the monthly fluctuations of photosynthetic biomass, and its nutrient content.

2.1. Needle-weight variation

Table 2 indicates the mean weight of a needle as a function of its age. During the first growing season, weight increases in parallel to growth. From November to February, all intense metabolic activity stopes in the needle, but this is not accompanied by a weight-loss. Metabolic activity starts again in March at the same time as a new generation of shoots begins, and remains significant in April and May. Then the weight of the needles decreases while the new generation is forming, and at the end of this second growing cycle, the 5 and 16-month-old needles have nearly the same weight. Lastly, at the renewal of growth in March, the 22-month-old needles also recover their metabolic activity again, which is expressed in a new increase in their weight, approximately the same as that observed in March of the preceding year (age 10 months).

2.2. Generalization

Knowing the weight of a needle as a function of its age, and the production and foliar biomass of the stand, it is possible to estimate the number of needles in the canopy, and monitor the fluctuations in their mass.

The foliar biomass was evaluated at 12.7 t ha^{-1} between February and June (Cabanettes, 1979), and consisted of 55.3 % (7 t ha^{-1}) one-year-old needles,

Table 2 - Increase of needle-weight as a function of age.

Age (month)	Month	Month mg	Increment mg
1	June	22.8	22.8
2	July	49.3	26.5
3	August	82.9	33.6
4	September	107.3	24.4
5	October	128.1	20.8
9	February	128.0	0 (- 0.1)
10	March	157.7	29.7
11	April	150.1	- 7.6
12	May	152.9	2.8
13	June	144.1	- 8.8
14	July	141 4	- 2 7
16	September	127,4	- 14 0
22	March	154.6	27.2
26	July	146.6	- 8.0

and 44.7 % (5.7 t ha^{-1}) two-year-old needles. The annual production was 7.3 t ha^{-1} (Cabanettes and Rapp, 1981 b). In this case, the two-year-old needles only amount to 5.4 t ha^{-1}. Litterfall was also evaluated (Rapp, 1983). The needle-fraction amounted to 6.1 t ha^{-1}, which is the equivalent of 7.3 t ha^{-1} of green material, taking account of a weight-loss of 17 % during sencescence (Cabanettes, 1979). Thus, a fraction of the litter, corresponding to 7.3 - 5.4 = 1.9 t ha^{-1} of green needles, consists of needles which have fallen to the ground before reaching the age of 2 years, i.e. during their first year. This confirms the data already obtained concerning the number of needles per shoot, which decreases from 193 to 181 from one year to the next. Figure 2 summarizes the distribution of foliage according to age and monthly development, both on the tree and in litter.

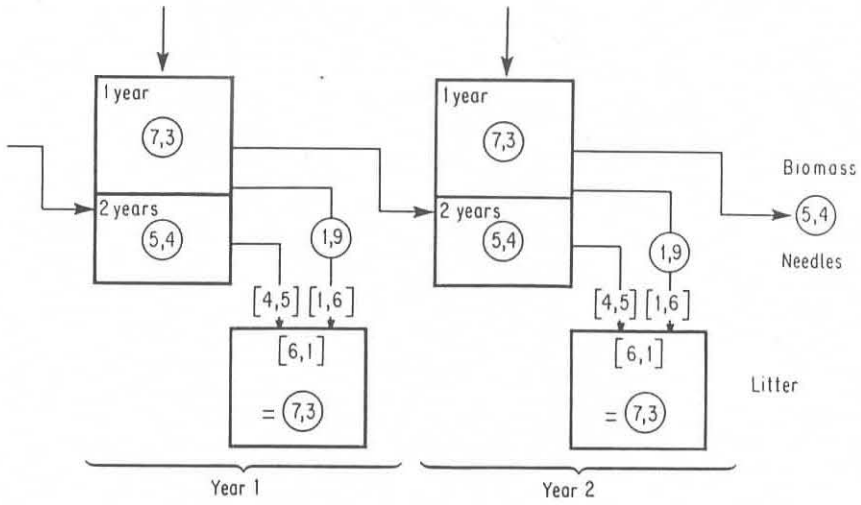

Figure 2. Model of the annual foliage cycle in the stand (t ha^{-1}).

0 : results expressed as biomass
[ ] : results expressed as litter.

However, biomass and needle-fall vary continuously as a function of the mechanisms of growth, senescence, and abscission. The biomass increment of the needles during the first year can be determined with relative precision by basing it on the number of needles in the stand. For one year, the production is 7.3 t ha^{-1} and the mean weight of a needle is 153 mg. This corresponds to 47.8 x 10^6 needles per hectare. Hence, the biomass of the needles at any one moment in time, "t", equals the mean weight of a needle at that moment, multiplied by 47.8 x 10^6. Table 3 shows the monthly development of foliar biomass during the first year. The reliability of this method is confirmed by the fact that the values thus obtained correspond closely to those determined directly during foliar biomass measurements (Cabanettes, 1979), which amounts to an average of 7 t ha^{-1} between February and June.

The monthly litterfall is also shown on the same table (Rapp, 1983), expressed as the weight of green material and the weight increment of needles

Table 3 - Monthly foliage production in a *Pinus pinea* L. stand (biomass and litter) - Results in t ha^{-1} $month^{-1}$

Month	Needle biomass 1 year	Needle biomass 2 years and more		Montly needle	Needles returned to the soil as litter *
June	1.1	7.3	4.7	13.1	0.7
July	2.4	7.3	2.4	12.1	2.3
August	4,0	7.3	1.0	12.3	1.4
September	5.2	7.3	0.3	12.8	0.7
October	6.1	7.1		13.2	0.5
November	6.1	6.9		13.0	0.2
December	6.1	6.8		12.9	0.1
January	6.1	6.7		12.8	0.1
February	6.1	6.6		12.7	0.1
March	6.7	6.3		13.0	0.3
April	7.2	5.9		13.1	0.4
May	7.3	5.4		12.7	0.5

* Calculated on the basis of monthly litterfall (Rapp, 1983) expressed as living material (litter + 20 %).

older than 12 months. In the latter calculation, we assumed that the last of the 2-year-old needles fall in September at the age of 27 months. The amount of 1-year-old needles on the tree can be estimated by deducting the monthly litterfall from the 5.4 t of needles present in May. The remaining 1.9 t ha^{-1} of litterfall (7.3 - 5.4), is deducted from the 1 to 2-year-old needles according to the rhythm of the monthly litterfall.

On the basis of these results, the monthly biomass of the needles can be determined, either totally, or according to age. Figure 3 summarizes the monthly development of the stand's canopy.

2.3. Nutrient content in the foliage

By taking the N, P, K, Ca and Mg contents in needles of different ages and the amount of foliage at the same moment, it is possible to calculate the

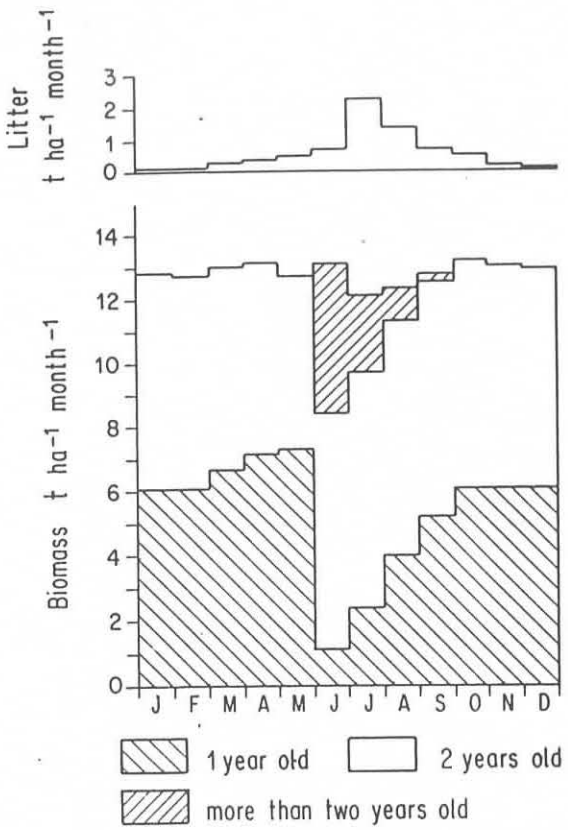

Figure 3. Monthly distribution of the foliage with respect to age.

monthly content of these nutrients in the canopy, and their fluctuation. Figure 4 shows the monthly variations of each of the five elements studied. These variations range from :

114.9 to 138.2 kg ha^{-1} for nitrogen (mean 124.9 ± 7.4)
88.8 to 140.9 " " for potassium (" 118.2 ± 13.4)
42.9 to 59.6 " " for calcium (" 48.3 ± 5.5)
17.9 to 22.3 " " for phosphorus (" 20.1 ± 13.4)
26.0 to 31.9 " " for magnesium (" 28.3 ± 5.5)

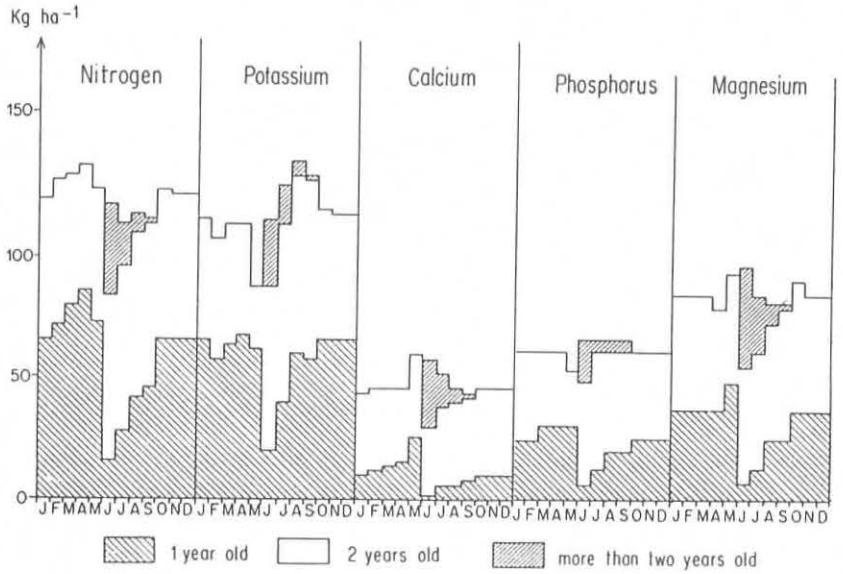
Kg ha⁻¹
Nitrogen
Potassium
Calcium
Phosphorus
Magnesium
150
100
50
0
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1 year old
2 years old
more than two years old

Figure 4. (a, b) - Monthly distribution of nutrients in the canopy according to needle-age.

The monthly total litterfall and needle-fall have been the object of a detailed study (Rapp, 1983). The return to the soil was calculated on the basis of these weight results and chemical analysis of the same samples. The monthly and total results are summarized in Table 4, both for the needles and for other litter fractions.

The 1.8 t of litter formed by material other than needles consists of 0.9 t ha^{-1} of wood and twigs, 0.3 t ha^{-1} of male inflorescences, and 0.6 t ha^{-1} of cones. Their return to the soil amounts to 10.9 kg ha^{-1} of nitrogen, 5.2 of potassium, 9.8 of calcium, 1.0 of phosphorus, and 1.5 of magnesium. The distribution among the three types of components is as follows :

	N	K	Ca	P	Mg
perennial component (wood)	3.6 kg ha^{-1} $year^{-1}$	1.0	8.4	0.2	0.6
male inflorescences	2.5	2.5	1.0	0.3	0.4
cones	3.8	1.7	0.4	0.5	0.5

Table 4 - Return of nutrients to the soil with litter fall (kg ha^{-1} $year^{-1}$ for the nutrient, t ha^{-1} $year^{-1}$ for the litter weight).

	Needles							Total litter						
	Litter weight	N	K	Ca	Mg	P		Litter weight	N	K	Ca	P	Mg
January	0.1	0.7	0.4	0.5	0.1	0.1		0.2	1.0	0.5	1.1	0.1	0.3
February	0.1	0.5	0.3	0.3	0.1	0.1		0.2	0.8	0.4	0.8	.0.1	0.1
March	0.2	0.5	0.9	1.2	0.3	0.6		0.3	2.0	1.2	1.6	0.4	0.7
April	0.3	1.7	1.1	1.7	0.3	0.8		0.4	2.3	1.4	2.2	0.4	0.9
May	0.4	1.8	1.3	2.0	0.3	1.5		0.6	3.1	2.4	3.1	0.4	1.2
June	0.6	2.8	3.2	3.2	0.5	1.5		0.9	5.1	4.9	4.3	0.7	1.9
July	1.9	6.2	7.9	11.8	1.6	5.7		2.1	7.3	8.4	12.6	1.7	5.5
August	1.2	4.6	3.7	7.4	0.8	3.2		1.3	5.4	4.1	8.0	0.9	3.3
September	0.6	2.8	2.8	2.9	0.4	1.2		0.7	3.4	3.0	3.8	0.4	1.3
October	0.4	2.2	1.7	2.3	0.3	0.9		0.6	3.1	1.9	3.7	0.4	1.0
November	0.2	1.3	0.8	1.1	0.2	0.5		0.4	2.1	1.0	2.3	0.3	0.6
December	0.1	0.7	0.4	0.5	0.1	0.2		0.2	1.1	0.5	1.2	0.2	0.3
Year	6.1	26.8	24.5	34.9	5.0	15.6		7.9	36.7	29.7	44.7	6.0	17.1

Table 5 - Monthly and annual fluxes of nutrients in the stand's foliage (kg ha^{-1}).

		JANS.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUGUST	SEPT.	OCT.	NOV.	DEC.	Year
N	Needles	124.9	131.3	134.8	138.2	117.8	121.7	114.9	118.0	116.7	128.5	126.7	125.8	
	Litter	0.7	0.5	1.5	1.7	1.8	2.8	6.2	4.6	2.8	2.2	1.3	0.7	
	Recycled	0.2				18.7		4.0						22.9
	Takon up		7.1	4.0	4.9		5.7		9.3	3.3	14.6	0.4	0.4	49.7
K	Needles	116.8	108.8	111.3	113.2	88.8	117.6	130.8	140.9	134.7	119.9	118.3	117.6	
	Litter	0.4	0.3	0.9	1.1	1.3	3.2	7.9	3.7	2.8	1.7	0.8	0.4	
	Recycled	0.4	7.6			23.3				2.5	12.0			45.8
	Takon up			2.8	2.8		30.1	16.4	18.0			0.1	0.1	70.3
Ca	Needles	44.6	45.9	46.5	46.5	59.6	58.6	52.5	45.1	42.9	46.7	45.7	45.2	
	Litter	0.5	0.3	1.2	1.7	2.0	3.2	11.8	7.4	2.9	2.3	1.1	0.5	
	Recycled	0.1						2.9						3.0
	Takon up		1.8	0.9	1.2	14.8	1.0		4.4	5.2	6.7	1.3	0.6	37.9
P	Needles	19.1	19.5	19.9	19.9	17.9	21.7	22.3	21.2	21.2	19.8	19.4	19.3	
	Litter	0.1	0.1	0.3	0.3	0.3	0.5	1.6	0.8	0.4	0.3	0.2	0.1	
	Recycled	0.1				1.7					1.0	0.1		2.9
	Takon up		0.5	0.5	0.3		4.1	1.1	0.5	0.8			0.1	7.9
Mg	Needles	28.3	28.1	27.4	26.2	31.0	31.9	27.1	26.7	26.0	29.3	28.8	28.6	
	Litter	0.2	0.1	0.6	0.8	1.0	1.5	5.4	3.2	1.2	0.9	0.5	0.2	
	Recycled	0.1		0.6	0.6			3.3						4.6
	Takon up					5.6	1.9		5.0	2.5	4.5	0.4	0.3	20.2

On the basis of the monthly fluctuations of nutrient elements contained in the foliage and the return to the soil of the same elements by needle-litterfall the monthly absorption of an element by the needles or its possible recycling to the perennial or reproductive components can be calculated using the following formula : (element in the needles, month n) - [(element in the needles, month n-1) - (element in the needle-litter, month n-1)] =

- uptake if the value is positive
- recycling, if the value is negative.

Table 5 includes these different parameters and indicates the monthly uptake and recycling of these 5 elements. Significant potassium and phosphorus uptakes are observed in June, the month during which the year's new needles begin to form. In the case of magnesium, two peaks can be seen in May and August, also related to the development of the photosynthetic system. The situation is different for calcium, which is particularly used by needles that have reached maturity. A very large uptake can be seen in May, indicating the use of this cation by one or two-year-old needles. But this calcium uptake has already started by the end of the growing period, and is intense in September and October of the first year when the needles are 4 and 5 months old respectively. Lastly, nitrogen's uptake is spread out over the whole year in a rather irregular fashion. The large uptake in February, which continues on into March and April, can be explained by the beginning of shoot, branch, and trunk-growth in that period. The same cannot be said for the high nitrogen uptakes in August and October. Also note that in the flow of these elements toward the needles, a significant decrease is observed in July and sometimes in August, with the exception of potassium. This is the result of a slight deficit in the stand's water supply during this period, which leads to decreased transpiration (Ibrahim, Rapp, Lossaint, 1982). The large potassium uptake during these same two months is related to the same physiological problem. This alkali plays an essential role

in stomatic regulation, which is one of the plant's major mechanisms for the adaptation to reduced availability of water.

The recycling from the needles to the perennial and reproductive components is very substantial in the case of potassium (65 % of the uptake). It represents mean values, for nitrogen and phosphorus respectively, of 46 % and 41 % of the uptake. On the other hand, magnesium (23 %) and especially calcium (8 %) undergo less recycling. This is easily explained for magnesium, since it is particularly used by the chlorophyllian components. However, the case of calcium is more complicated. This element is fixed by the needles and also in large quantities by the woody tissue. The latter fraction must hence be taken up directly from the water flux by the woody tissue. With respect to the timing of redistribution, a significant recycling of nitrogen, potassium, and phosphorus occurs in May. Considering the chemical composition of the shoots, which are in full growth in this month, it can be supposed that there is a translocation from the one or two-year-old needles to the shoots.

3. Annual shoot production

Shoot production amounts to 1.4 t ha^{-1} between the zero-point in February and the end of October (Cabanettes and Rapp, 1981 b). This period can be subdivided into two phases. The first, from February to May, is characterized by the elongation of the shoots. The second, from June to October, corresponds solely to weight-increase, the length remaining constant. As of November, growth is finished. Between October and March of the following year, the weight of one centimeter of shoot increases from 294.4 to 314.5 mg.

Figure 1 permits a calculation of the monthly shoot length during the first phase. In the second phase, the mean shoot weight is successively : 153.8 mg in June and July, 223.8 mg in August, and then 294.4 mg in September and October.

By taking the final production of 1.4 t ha^{-1} in October, and successively combining the measurements of elongation and then weight-increase, the following values are obtained from February to October :

0.02 t ha^{-1}	in February
0.09 "	in March
0.22 "	in April
0.62 "	in May
0.62 "	in June
0.62 t ha^{-1}	in July
0.90 "	in August
1.37 "	in September
1.37 "	in October

Since the chemical composition of the shoots is known for each of these months (Table 1), one can determine the monthly and then the annual immobilization by these components, which amounts to :

8.9 kg ha^{-1}	of nitrogen
8.9 "	of potassium
6.2 "	of calcium
1.4 "	of phosphorus
3.1 "	of magnesium

4. Annual wood production

The term "wood" includes the weight-increases in branches, trunks, and roots during the course of the year. These increases amount to 5.8 t $ha^{-1} year^{-1}$, comprising 3.8 t ha^{-1} of stem wood, 0.9 t ha^{-1} of branches, and 1.1 t ha^{-1} of roots (Cabanettes and Rapp, 1981 b).

The monthly evaluation of stem wood production was based on the mean monthly increase in the circumference (Fig. 1) of the trunks of fifteen repre-

Table 6 - Monthly production of stem wood, branches, and roots (t ha^{-1}).

Month	Sem wood = trunks		Branches	Roots	Perennial total
	xylem	bark			
January	0·12	0·02	0·03	0·03	0.20
February	0.12	0.02	0.03	0.03	0.20
March	0.25	0.05	0.07	0.09	0.46
April	0.86	0.19	0.25	0.31	1.61
May	1.48	0.33	0.43	0.53	2.77
June	1.98	0.44	0.57	0.69	3.68
July	2.10	0.47	0.61	0.75	3.93
August	2.22	0.50	0.64	0.79	4.15
September	2.73	0.61	0.79	0.97	5.10
October	3.10	0.70	0.90	1.10	5.80
November	-	-	-	-	-
December	-	-	-	-	-

sentative trees in the stand between January and October. In addition, we took account of the fact that the 3.8 t ha^{-1} of stem wood consists of 3.1 t ha^{-1} of xylem and 0.7 t ha^{-1} of bark.

The same production rhythm was applied to branches and roots, for which there was no direct observation. All the monthly observations between January and October are shown in table 6.

On the basis of these weight results, we calculated the uptake of the five nutrients, using the following mean percentages (Rapp and Cabanettes, 1980) :

	N	K	Ca	P	Mg
Trunks					
xylem	0.11 %	0.11 %	0.27 %	0.03 %	0.04 %
bark	0.27	0.17	0.99	I.08	0.13
Branches	0.37	0.24	0.65	0.05	0.11
Roots	0.14	0.22	0.38	0.05	0.11

Table 7 - Nutrients immobilized monthly by perennial mineral-mass increase (kg ha^{-1})
- The results in july are negative for N, P and K. This corresponds to the shrinkage phenomenon observed in the trunk (Fig. 1).

	N	K	Ca	Mg	P
January	0.35	0.27	0·92	0.13	0.10
February	0.23	0.26	0.05	0.04	0.05
March	1.22	1.25	1.14	0.30	0.23
April	3.40	3.30	5.13	1.05	0.75
May	6.31	6.85	6.19	1.78	1.20
June	1.55	2.01	4.05	0.38	0.15
July	{1.19}	{1.98}	1.91	0.44	{0.05}
August	3.12	0.47	2.64	1.18	0.37
September	1.78	4.75	7.46	1.30	0.50
October	2.33	0.91	2.01	0.94	0.58
November	0	0	0	0	0
December	0	0	0	0	0
Total year	19.10	18.10	31.50	7.50	3.90

Table 8 - Montly nutrient requirements of the vegetative components (kg ha^{-1})

	N	K	Ca	P	Mg
January	Q.2	0	0·8	0	0
February	7.3	0	1.9	0.6	0.1
March	5.2	4.0	2.0	0.7	0
April	8.3.	6.1	6.2	1.1	0.5
May	0	0	21.0	0	8.3
June	7.3	32.1	5.1	4.2	2.3
July	0 ·	14.4	0	1.0	0
August	12.4	18.5	7.0	0.9	6.2
September	5.1	2.3	14.7	1.3	3.8
October	16.9	0	8.7	0	5.4
November	0.4	0.1	1.3	0	0.4
December	0.4	0.1	0.6	0.1	0.3
Total	63 5	77 6	67 3	9 9	26 3

Table 7 summarizes the annual immobilization of the 5 elements with respect to the increment of perennial mineral-mass.

5. Nutrients used monthly by the vegetative components

By combining the data in Table 7, which represents the requirements of the perennial components, with the uptake of the same elements by the needles, which is shown in Table 5, the monthly uptake required for the vegetative life can be determined in a stand of *Pinus pinea* L. This amounts to adding the quantities immobilized by the perennial components to those taken up by the chlorophyllian components when there is uptake by the needles. In the case of the redistribution of any of these elements from the needles to other tree components, the redistributed quantities are subtracted from those elements immobilized by the perennial portions of the phytomass. The values for the monthly and annual requirements of these 5 nutrients are shown in Table 8 and Figure 5. It can be seen that uptake corresponds closely to the growth rhythms of the various components shown in Figure 1. November, December and January are characterized by a very low uptake. As of February, the beginning of trunk-thickening corresponds to a significant increase in uptake, which continues into June, the period when new needles are produced. In July, drought is accompanied by a cessation of wood production, or a certain shrinkage, which corresponds to a decrease in uptake. Lastly, from August to October, production begins again at a lower intensity, indicated by a renewed nutrient uptake from the soil.

However, as was already observed in the needles, the distribution of monthly uptake in the phytocenosis also varies with respect to the different elements. Thus, maximum calcium uptake occurs in May and then in September, and corresponds to trunk and shoot growth in May, and trunk growth alone in September. In the latter month, the shoots have finished their elongation, but still increase in weight, thus fixing calcium in the cell walls.

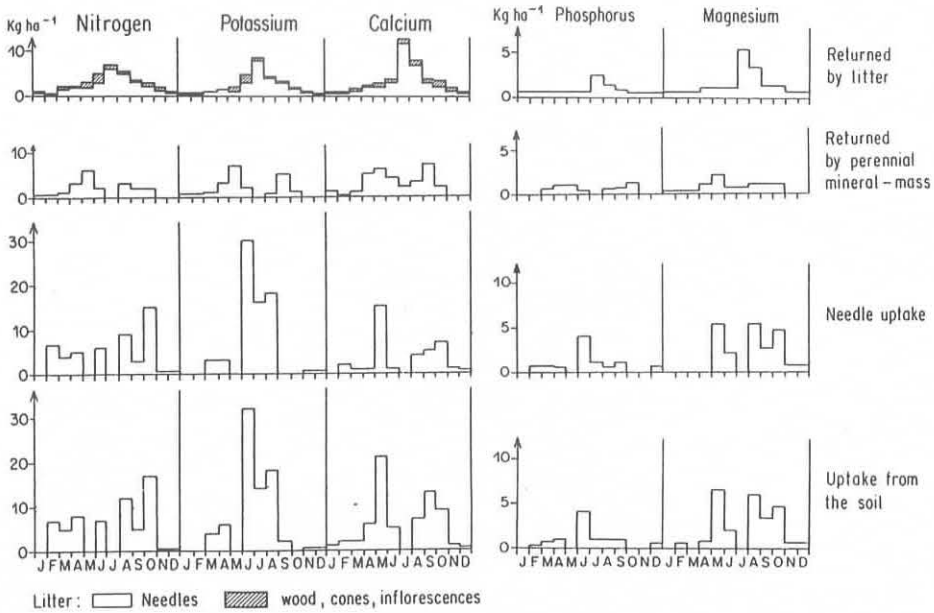
Kg ha⁻¹ Nitrogen
Potassium
Calcium
Kg ha⁻¹ Phosphorus
Magnesium
Returned by litter
Returned by perennial mineral - mass
Needle uptake
Uptake from the soil
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
J F M A M J J A S O N D J F M A M J J A S O N D
Litter: Needles wood, cones, inflorescences

Figure 5. (a, b) - Monthly values for the nutrient fluxes between the phytocenosis and the soil, on one hand, and between the assimilating components (needles) and the perennial components (trunks, branches, shoots and roots) on the other.

Potassium is especially absorbed between June and August, phosphorus in June. These two elements are essentially used by the needles, which have their highest growth-rate in this period. The important role played by potassium in stomatic regulation should also be considered, as mentioned above. This is also the case for magnesium, whose uptake starts in May with the beginning of the year's shoot production.

Nitrogen uptake is the only phenomenon which is difficult to explain. Maximum uptake appears to occur between August and October, which does not correspond to the most active period of the species. It is possible that this essential element is used later, in an assimilated protein form, during growth in successive years.

6. Nutrients used by the reproductive components

Contrary to the procedure up to this point, it is not possible to calculate the monthly requirements of male inflorescences and cones. Altogether these components represent a production of 4 t $ha^{-1}year^{-1}$, consisting of 0.3 t ha^{-1} of male inflorescences and 3.7 t $ha^{-1}year^{-1}$ of cones (Cabanettes and Rapp, 1981 b). This production corresponds to an immobilization of 12.3 kg $ha^{-1}year^{-1}$ of nitrogen, 11.6 of potassium, 4.8 of calcium, 1.2 of phosphorus and 3.7 of magnesium.

The distribution between inflorescences and cones, expressed in kg ha^{-1} is as follows :

	N	K	Ca	P	Mg
male inflorescences	2.7	2.4	1.1	0.3	0.4
cones	9.6	9.2	3.7	0.9	3.3

Since these components do not themselves assimilate, the quantities of immobilized nutrients must essentially represent recycling from the needles.

It should also be noted that although the elements used by the inflorescences are mostly found in the corresponding litter, the same correspondence does not exist for the cones. This arises chiefly from an underestimation of the cones in the litter harvest, due to the spatial heterogeneity of this component's litter.

7. Forest budget

On the basis of the total of the various translocations and of the distribution within the tree of the five nutrients studied, a model can be made for the budgeting of by the phytocenosis.

To complete the data on the different fluxes which have been quantified above, we also indicate the more static compartments formed by the perennial mineral-mass and the needle mineral-mass, since the latter is composed of a

pool of nutrients which undergoes a complete rotation every 24 to 27 months.

The first subdivision was the subject of a previous study (Rapp and Cabanettes, 1980) in which the following values were determined :

337.7 kg ha^{-1} of nitrogen
277.7 " " of potassium
772.3 " " of calcium
71.8 " " of phosphorus
129.8 " " of magnesium

With respect to foliage, the values in May give the best image, corresponding to 7.3 t ha^{-1} produced annually and 5.4 t ha^{-1} of two-year-old needle biomass.

The corresponding values for the five nutrients assayed are :

	needles : 1 year	needles : 2 years	total
N	73 kg ha^{-1}	44.8 kg ha^{-1}	117.8 kg ha^{-1}
K	61.3 "	27.5 "	88.8 "
Ca	27.7 "	31.9 "	59.6 "
P	10.9 "	7.0 "	17.9 "
Mg	15.3 "	15.7 "	31.0 "

On the basis of this data and that of Tables 4, 5, 7 and 8, a circulation and distribution model can be constructed for each element in the phytocenosis (Figures 6 to 10) representing its budget and cycling patterns in the stand.

These models display a certain number of innovations, resulting partly from a determination of uptake on the basis of the annual development of the different tree-components and resulting partly from the estimation of the input and output fluxes in the foliage. These same evaluations enable us to demonstrate possible redistributions of certain nutrients, especially nitrogen and phosphorus, between different needle generations.

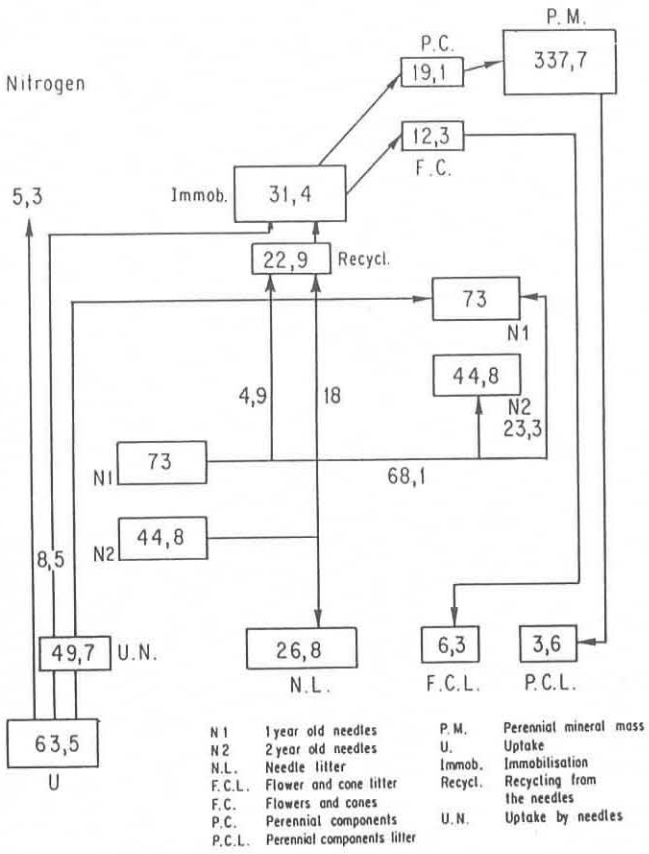

Figure 6. Model of nitrogen fluxes in the plant-soil interface and in the translocations within the plant.

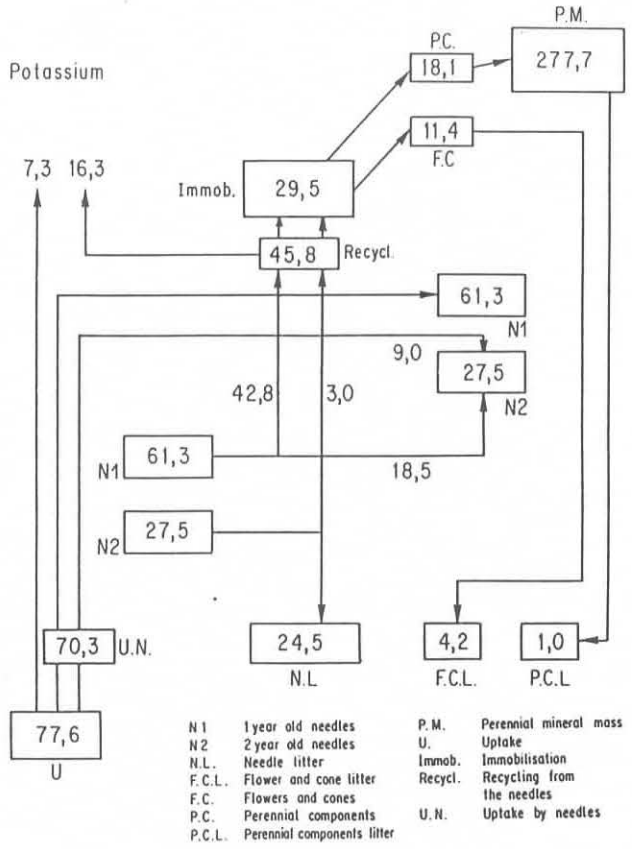

Figure 7. Model of potassium fluxes in the plant-soil interface and in the translocations within the plant.

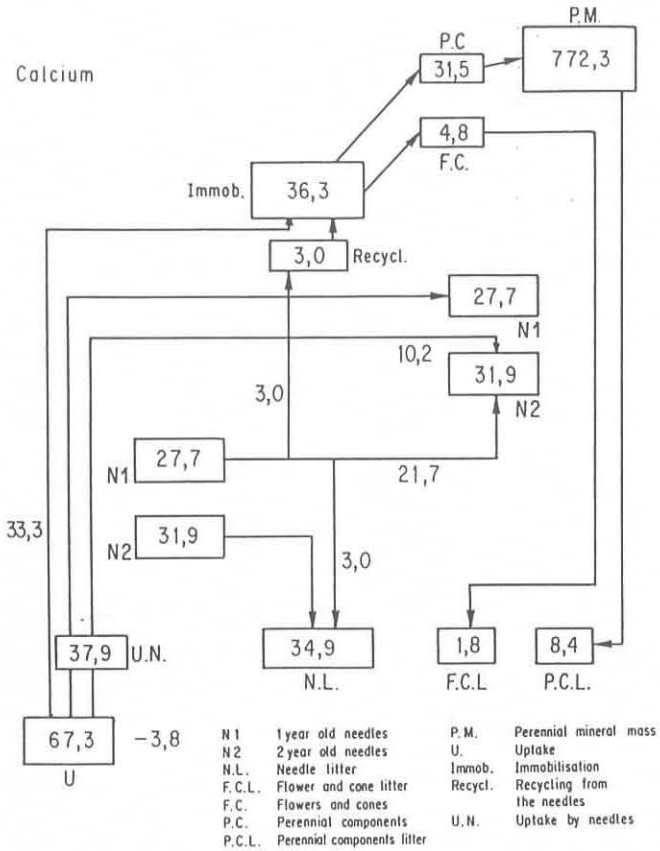

Figure 8. Model of calcium fluxes in the plant-soil interface and in the translocations within the plant.

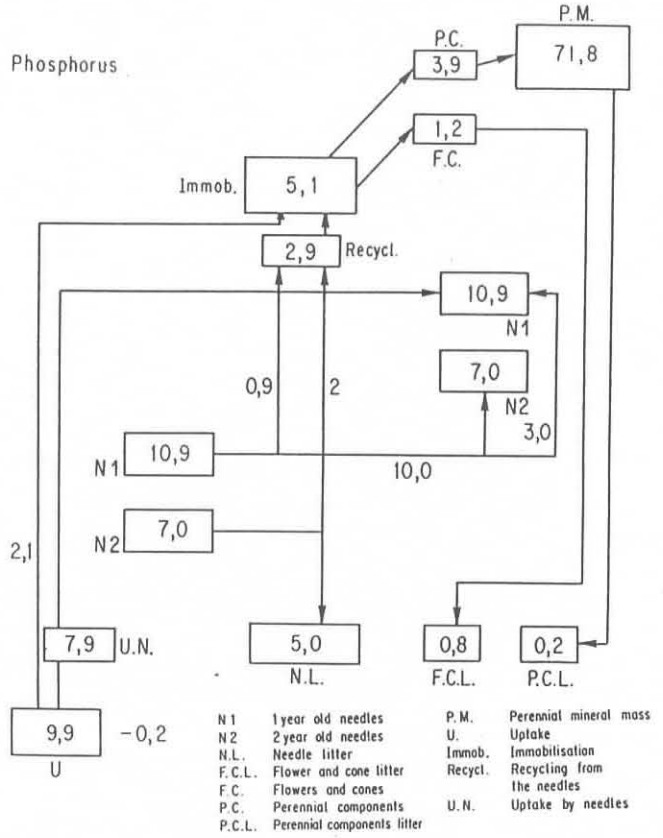

Figure 9. Model of phosphorous fluxes in the plant-soil interface and in the translocations within the plant.

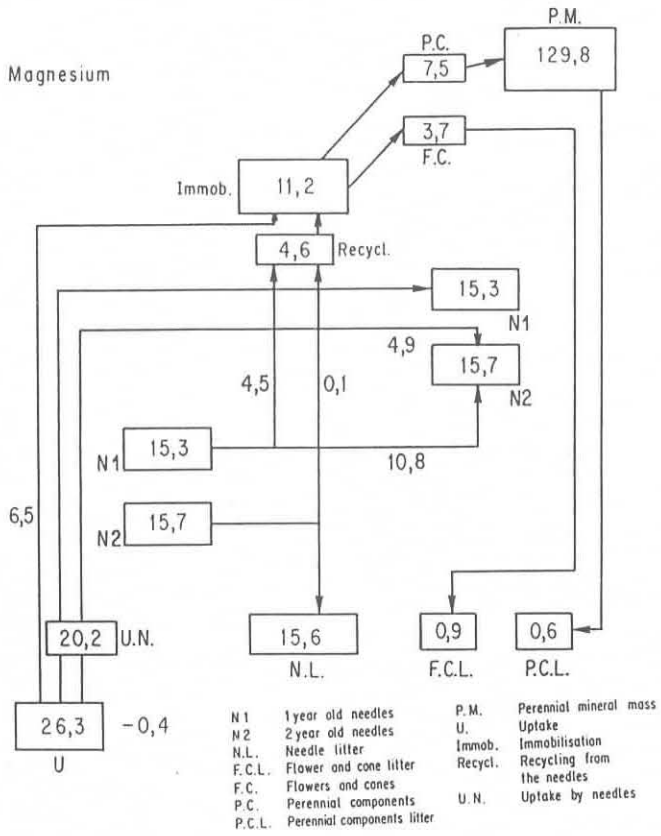

Figure 10. Model of magnesium fluxes in the plant-soil interface and in the translocations within the plant.

With regard to the vegetation, the cycles of these five nutrients are in equilibrium. The equilibrium is complete for P and Mg, with a difference on the order of 2 % between the different evaluations of their uptakes and requirements. Even the 5 % difference observed in the case of calcium does not diminish the reliability of the method used to quantify the nutrient cycling, considering that it is based on field observations, which always involve a rather large margin of uncertainty.

Even in the cases of nitrogen and potassium, where the distortion between the different approaches reaches 9 %, the final result remains largely positive, even if cause of this 9 % cannot be defined in the stand. The evaluation of potassium also shows the importance of the recretion phenomenon for this element, representing a return to the soil of 16.3 kg $ha^{-1} year^{-1}$ via the through-fall process.

CONCLUSION

This study of the biomass variations and the cycling of five nutrients in a *Pinus pinea* L. stand, based on observations made at the relatively short time-intervals of one month, has led to a certain number of new results, both with respect to annual evaluation and to seasonal dynamics.

The first observations concern the development of phytomass with respect to time. They represent a transition from classical phenological observations to the quantification of growth components. They make it possible to determine the perennial phytomass increment during the course of the growth cycle, as well as fluctuations in the foliage.

All these data related to biomass can be transposed to the perennial or foliar mineral-mass in terms of the five nutrients studied. The approach also permits a definition and quantification on the basis of the monthly conditions of a certain number of fluxes between the phytocenosis and the soil, or between

the different tree components. It is thus possible to calculate the nutrient requirements of a stand, to distinguish the uptake of certain quantities of nutrients in the foliage or their recycling to non-chlorophyllian components by way of photosynthesized assimilates. For certain nutrients, this approach allows a direct estimation of recretion, which is one of the mechanisms involved in through-fall. Finally, in the present case, which concerns conifers with multiannual leaving needles, the method provides certain indications about the foliar turnover of nutrients. Evaluations of the translocations between one and two-year-old needles, litter, and reproductive and perennial components indicate a possible redistribution of certain nutrients from the two-year-old needles to younger needles that are still growing.

In general, these observations show that a study which is more detailled with respect to time, and which deals with different compartments of the phytocenosis, or even of the ecosystem, opens new horizons for the refinement of quantitative evaluations of the different compartments and fluxes in the biogeochemical cycles. In addition, this approach allows an examination of the role and importance of certain parameters of the biogeochemical cycles with respect to time, especially with regard to the soil-plant interface and the phytocenosis itself.

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